BEHAVIOR AND HABITAT USE OF BREEDING NORTHERN HARRIERS IN SOUTHWESTERN IDAHO

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ABSTRACT.—Radiotelemetric and visual monitoring of four breeding pairs of the Northern Harrier (*Circus cyaneus*) in predominantly shrub-steppe habitat of the Snake River Birds of Prey Area, Idaho, indicated that harriers used riparian and cultivated habitats disproportionately. As alfalfa growth approached 46 cm height, males shifted from predating voles (*Microtus* sp.) in alfalfa fields to the Western Whiptail (*Cnemidophorus tigris*) in open shrub-steppe habitat. Mean minimum home ranges of males were estimated at 15.7 km² while those of females were estimated at 1.13 km². Males ranged up to distances of 9.5 km from nests. Males hunted most intensively in the second week after hatching. Females did not hunt until the third week after hatching. During most of the day, both sexes rested or preened <0.5 km from nests. Varying home range sizes in this and other studies may be a function of harrier responses to differing habitat structures and prey availability or vulnerability to capture.

Breeding behavior of the Holarctic Northern (Hen) Harrier (*Circus cyaneus*) has been studied and discussed by Breckenridge (1935), Bent (1937), Brown and Amadon (1968), Hamerstrom (1969) and Watson (1977). These and other studies showed that male participation in the breeding effort is limited primarily to provisioning prey for their mates and young, with incubation or care of young rarely recorded (Bildstein 1979; Thompson and Cornely 1982). Male abandonment of the breeding effort prior to fledging of young is not uncommon and is usually associated with increased hunting activity by females (Hamerstrom 1969; Watson 1977).

Few studies have attempted to quantify male and female harrier behavior and activities related to habitat utilization in upland areas. This study was conducted from March through July 1981 with the objective of determining breeding activities in a habitat type not typically associated with harriers.

STUDY AREA AND METHODS

Four nesting pairs of harriers were selected in the Snake River Birds of Prey Area (BOPA) in southwestern Idaho, a 338 778 ha sanctuary within the Upper Sonoran life zone of the Great Basin Region characterized by a cold desert physiognomy and climate (Odum 1971; USDI 1979). Nesting or pair-bonded harriers were located using methods discussed by Hamerstrom (1969, 1986). Emphasis was placed on determining behavior and activities of breeding male harriers occurring within the BOPA. Precautions were taken to avoid investigator disturbances near nests [i.e., trampling vegetation and creating paths for predators to follow (Fyfe and Olendorff 1976)].

Habitats were categorized into six types: water, riparian, shrub-steppe, cultivated fields, abandoned fields, and barren soils. Water habitats were open waters of the Snake River, reservoirs, and irrigation systems. Riparian habitat consisted primarily of pampas grass (*Phragmites communus*), bulrush (*Scirpus* sp.), stinging nettle (*Urtica* sp.), willow (Salix sp.), and tamarisk (Tamarix pentandra). Greasewood (Sarcobatus vermiculatus) formed a transitional zone between riparian and shrub-steppe habitats and was included in the riparian habitat category. Shrub-steppe was the dominant upland habitat, consisting primarily of big sagebrush (Artemisia tridentata), cheatgrass (Bromus tectorum), and shadscale (Atriplex confertifolia) associations. A variety of crops made up cultivated fields, primarily alfalfa (Medicago sativa), wheat (Triticum aestivum), and sugar beets (Beta vulgaris). Cultivated fields were dependent on water through sprinkle or flood irrigation. Abandoned fields were dry fallow cultivated fields invaded by halogeton (Halogeton glomeratus), cheatgrass, and Russian thistle (Salsola kali). Barren soils were a variety of mine tailings, gravel pits, cliffs, and lava beds.

Habitat analyses were made by overlaying 1:24000 USGS topographic maps with a grid. Each square size represented 0.405 ha and was assigned a habitat type determined from aerial photographs, vegetation maps provided by the Boise District Office of the Bureau of Land Management, and from field observations. A circular area of approximately 200 km² was analyzed surrounding each of the study nests. On this basis, habitat percentages were calculated in order to detail harrier habitat utilization.

Selected alfalfa fields in the study area where harriers were observed hunting were measured for height from the ground along linear transects of 10 points. Cutting schedules were observed and recorded.

Six harriers were captured using a variety of techniques. Two males and two females were captured using a noosehalo (Scharf 1968) and a mounted Great Horned Owl (Bubo virginianus) on a portable one m high, placed 3-10 m from the suspected nest. One male was captured using an octagonal bal-chatri (Erickson and Hoppe 1979) with a Montane Vole (Microtus montanus) as bait. Another male was captured using a mist net set ≥ 1 m behind a mounted owl. A dho-gaza and mounted owl (Hamerstrom 1963) attracted several adult harriers but failed to result in any captures. Harriers may have detected dho-gazas or mist nets due to motion caused by prevalent winds. A wire dome with monofilament nooses (Burke 1979) or bownet (Hamerstrom 1969) placed over the nest was not used due to possible abandonment of eggs or young (Hamerstrom 1969).

Each individual captured was measured, weighed, and aged (Hamerstrom 1968). Colored plastic and USFWS bands were placed on the legs of each harrier, and a radio transmitter was attached to a central rectrix using techniques described by Dunstan (1973), Beske (1978), and modified by Martin (unpubl.). Transmitters used were AVM SM-1 units operated at 164 MHz weighing about five g when encased in dental acrylic. Transmitter whip antennas were trimmed to about 200 mm. Receivers were AVM LA-12 units with 10 subchannels, used alternately with three-element Yagi or Adcock antennas.

Prior to capture efforts, monitoring of harrier activities began in March during courtship and nest building. Distinctive markings and plumages (such as moulting or color patterns) were used to distinguish individuals. After radiotagging harriers, behavior and habitat use were sampled instantaneously (Altmann 1974) at 10-min intervals from 0500-2200 H (MST). Monitoring was conducted in 17hr blocks rotating once every seven d to each of the nests. The sampling effort was equal through all time periods of the day for the length of the study. Emphasis was placed on tracking males of a given nest as I assumed they would be far ranging, hunting for themselves and their mates, while females remained at the nests (Watson 1977). When a repeated direction of travel to and from the nest could be determined, alternate tracking days were spent in the suspected hunting areas and the nest. When possible, contact between two investigators was maintained by twoway radios. One investigator always remained near a given nest in the event that visual or radio contact was lost. In this manner, lost contact could be regained as the male harrier returned to a nest with prey and female behavior and activities could be monitored concurrently with males.

Home ranges were determined using the non-statistical minimum polygon method (Mohr 1947; Jennrich and Turner 1969). Radio telemetry was used primarily to assist in visually locating a harrier within a given habitat type, then observe its behavioral activities as suggested by Craighead et al. (1963) and Mech (1983). Radio triangulated positions (Mech 1983) were used to clarify harrier locations when necessary. All missed data points were eliminated from statistical analyses.

Harrier activities were placed into classes based on a scheme similar to those used by Linner (1980), Schipper (1977), and Bildstein (1982) [i.e., loafing (perching, resting, or preening), feeding, agonistic interactions (both intra- and interspecific), soaring or gliding, hunting flights (either border following or quartering), and other flights (including powered transit or high flights)]. Starting, ending, and duration of flights or activities, prey deliveries, prey items identified, and compass directions of travel to and from the nests were recorded.

Nesting chronology of each nest was determined by backdating the first prey taken into the nest, indicating hatch of eggs (Hamerstrom 1969). Due to the close proximity of two of the study nests, it was possible to observe harrier behavior and activities concurrently, noting initial prey deliveries to newly hatched young, without interfering with the established monitoring schedule. In addition, two of the nests occupied by radio-tagged harriers were examined to determine the age of young by weight and length of primary feathers (Munoff 1963; Hamerstrom 1968; Scharf and Balfour 1971).

Activities and habitat utilization of individuals were combined after synchronizing nesting chronologies into similar composite categories for statistical analyses. Statistical methods used are from Snedecor and Cochran (1967). A breeding effort was assumed to commence with the laying of eggs (through incubation of about 30–32 d), and ending about 35 d after hatching (with the young capable of flight), or about 70 d total (Hammond and Henry 1949; Hamerstrom 1969). After hatching of eggs, activities and behavior were broken into seven-d units for analysis. For some analyses, sample sizes were inadequate to list in weekly increments and were grouped into three major phases of breeding: incubation, brooding (from hatch to the end of the second week), and post-brooding (from the start of the third week to the end of the fourth week or as young fledged) (Watson 1977).

Results

Activities and Behavior—Males. Males were observed hunting at first light (± 30 min prior to sunrise). No prey deliveries were recorded before 0530 H (MST) and only one prey delivery was observed after 1900 H (MST). Prey deliveries/d peaked from 0900–1200 H (MST) and this pattern remained constant throughout the breeding season (Fig. 1). Copulations associated with prey given to females were observed for 15.6% of the total prey deliveries by males (N = 96), 48.0% occurring prior to 0900 H (MST), 35.0% from 0900–1200 H (MST), and 17.0% from 1200–1500 H (MST). All copulations observed were in association with prey deliveries and continued until day 15 of incubation.

The number of prey items delivered/d by male harriers to the nest or females peaked during the second week post-hatching. Concurrently, intervals between prey deliveries shortened and observed hunting activities increased (Fig. 2). For the entire season, the males delivered an average of 3.5 prey items/d to the female or nest. Prey deliveries ranged from one to three items/d during courtship and incubation, to a maximum of seven items/d during brooding, and decreasing to two to three items/d as chicks approached fledging. Male harriers were in flight during 52% of total observations. Only 20% of male flight activities could be classed as hunting behavior (Table 1).

Early in the season males spent most of their time loafing near nests (Tables 1 and 2). If monitoring had been conducted on a 24-hr basis, it is probable that the number of observations of males near nests would have been greatly reduced. At least one male

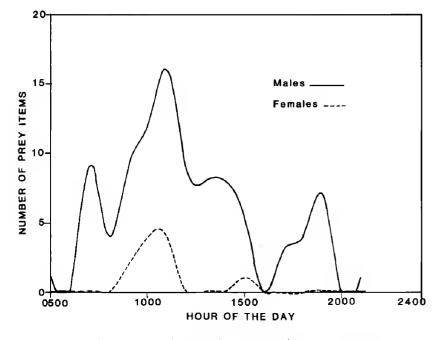


Figure 1. Number of prey deliveries/hour of the day for males and females.

did not roost within two km of the nest from the onset of incubation. After eggs hatched, the time males spent near nests decreased more rapidly than females. Foraging sorties by male harriers of 4.5-9.5 km were routinely observed. As the breeding season progressed, harriers tended to range farther, but these observations could not be quantified before the study terminated.

Flights to and from nests followed certain compass bearings that were traveled repeatedly throughout the nesting season at at least two of the study nests. Flight patterns were established during the courtship and nest building period, prior to radio-tagging. Due to nesting failures, observations were not completed for the other two nests.

Male agonistic interactions observed were pri-

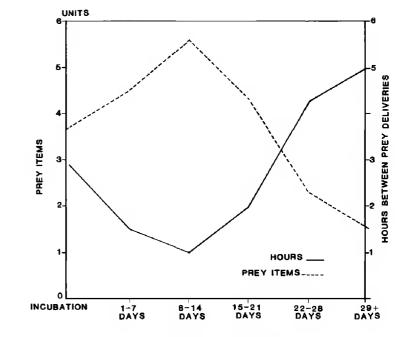


Figure 2. Frequency and number of prey items delivered to nest or female by male Northern Harriers

marily with other male harriers near nests (73.1%, N = 82). Most of these interactions occurred early in the season as territories were being established. Interactions with neighboring males and females declined through the breeding season. However, reaction to other harriers approaching the nest territory, even from nearest neighbors, always resulted in vigorous pursuit. Males defended an area of about 0.78 ha with the nest at the center. Borders between territories were often defined by vegetation changes or height differences, fence lines, or topographic features. Aerial talon-grappling described previously by Craig et al. (1982) was observed three times and these were the only intraspecific interactions observed away from nests.

Interspecific encounters included the pirating of

Nesting Events	Percent Time ^a					
	LOAFING	Hunting ^b	Feeding	Aggression	Soaring	Other Flights ^c
Incubation	53	15	2	2	10	18
Brooding	30	34	2	2	8	24
Post-brooding	<u>55</u>	<u>12</u>	2	2	3	28
Total for season	46	$\overline{20}$	$\overline{2}$	2	7	$\overline{23}$

 Table 1. Activities of male harriers in relation to nesting events.

^a Based on 688 visual or radio contact locations at 10-min intervals from a total of 2256 tracking intervals spent in the field (29.6% actual) and excludes observations of male activities between intervals.

^b Hunting activities included edge following and quartering flights.

^c Other flights were all flights determined not to be hunting or soaring (i.e., gathering nest materials, courtship, and high or transit flights).

	Percent Activities ^a			
– Distance from Nests	MALES	FEMALES		
<0.5 km	42.3	85		
0.5–1.0 km	23.9	11		
1.0–2.0 km	7.7	4		
2.0-3.0 km	11.3	0		
3.0-6.0 km	8.5	0		
>6.0 km	6.2	0		

Table 2.Harrier activities in relation to distance fromnests for the total breeding season.

^a All activity categories combined, based on 688 male and 250 female instantaneous samples at 10-min intervals, plotted on topographic maps.

a large unidentified prey item from a flying Redtailed Hawk (*Buteo jamaicensis*). Males appeared most aggressive towards intruders early in the breeding season, just prior to or just after start of incubation.

Activities and Behavior—Females. Hunting by female harriers was not observed prior to the third wk post-hatching (Table 3). Females were observed routinely for 10–15 min from 0700–0730 H (MST) in preening bouts or low flights near nests (<100 m) from the start of incubation through the second wk post-hatching. The only other time females were observed away from the nests was for food transfers from mates or to assist mates or neighboring harriers in attacking intruders (Powers et al. 1984). After the beginning of the third wk post-hatching, females were observed hunting from 0600–2120 H (MST). Female prey deliveries tended to follow the male prey delivery pattern from mid-morning to midafternoon (Fig. 1). Frequency or number of prey

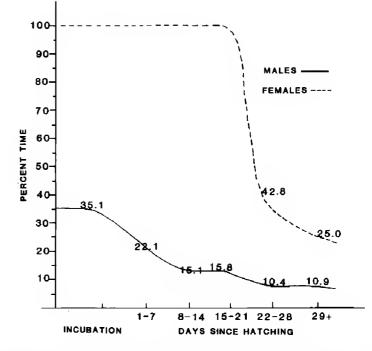


Figure 3. Time male and female harriers spent <0.5 km from nest site.

deliveries by females could not be determined quantitatively due to emphasis on monitoring male activities. Additionally, female activities during the incubation period were not determined (Fig. 3).

From the beginning of the third wk post-hatching, females ranged progressively farther from nests but never as extensively as males (Fig. 3). The longest flight observed by a female harrier was 600 m.

Flights to and from nests followed specific compass bearing, in patterns similar to males; however, female direction of travel differed from that of males. One harrier pair was observed flying to and from the nest in opposite directions. Females continued these flight patterns during courtship and nest building, and while hunting for themselves and young.

Intraspecific interactions involving females were oriented more towards other females (43.3%, N =

 Table 3.
 Activities of female harriers in relation to nesting events.

Nesting Events	Percent Time ^a					
	Loafing	Hunting ^b	Feeding	Aggression	Soaring	Other Flights ^c
Incubation	_					_
Brooding	79	0	2	1	1	17
Post-brooding	<u>64</u>	8	3	1	2	22
Total for season	46	4	3	1	2	19

^a Based on 250 visual or radio contact locations at 10-min intervals from a total of 264 tracking intervals spent in the field (94.7% actual) and excludes observations of females' activities between intervals.

^b Hunting flights included edge following and quartering flights.

^c Other flights were all flights determined not to be hunting or soaring (i.e., gathering nest material, courtship, and high or transit flights)

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	HABITAT TYPES ^a						
Distance from Nests	WATER ^b	RIPARIAN	Sage	Culti- vated	Abandoned Field	Barren Soils	
			% Habit	at Types			
Nest–0.5 km	26.6	22.6	46.7	1.0	3.1		
0.5–1.0 km	11.3	27.1	42.2	13.7	2.9	2.8	
1.0–2.0 km	37.7	16.2	25.3	20.8			
2.0–3.0 km	16.1	12.7	45.5	20.8	2.6	2.3	
3.0–6.0 km	2.5	3.1	74.9	17.2	1.2	1.1	
>6.0 km	<u>1.1</u>	1.0	77.9	<u>18.0</u>	<u>1.0</u>	<u>1.0</u>	
Total habitat types	6.9	5.9	67.5	17.9	1.4	0.3	
	% Male Habitat Use by Distance ^c						
Nest–0.5 km	5.5	81.8	_	1.8	10.9		
0.5–1.0 km	2.0	25.8	6.5	36.7	29.0		
1.0–2.0 km	20.0	10.0	50.0	20.0		_	
2.0-3.0 km	6.6	20.0	66.7	6.7			
3.0-6.0 km	—		45.5	54.5			
>6.0 km			<u>12.5</u>	87.5			
Total habitat use ^d	4.5	43.9	17.7	21.3	11.5	—	
	Male Habitat Use Related to Nest Events						
Incubation	3.0	48.0	7.0	21.0	21.0	—	
Brooding	4.0	18.0	42.0	24.0	12.0		
Post-brooding	4.0	27.0	38.0	23.0	4.0	_	
Total activities per habitat							
type for season ^d	4.9	33.3	28.5	22.8	10.6	—	

Table 4. Habitat types surrounding study nests in the Snake River Birds of Prey Area, and male harrier habitat utilization.

^a Percentage based on 200 km² area surrounding study nests determined from aerial photos, vegetation maps, and on-site inspections.

^b Harrier use of water habitat limited to over water flights to and from terrestrial habitats.

^c Male harrier habitat use determined from 688 instantaneous samples, using radio triangulation or visual contacts.

^d Error in total male harrier habitat use and activities due to differences in computation and is not statistically significant.

90) than males (21.7%, N = 90). Most intraspecific encounters occurred early in the season and females defended identical areas as males. Male-female interactions of mated pairs were excluded from consideration.

Females were most aggressive towards interspecific intruders, such as the Great Blue Heron (Ardea herodias) (6.5%, N = 90), Canada Goose (Branta canadensis) (4.3%, N = 90), and American Coot (Fulica americana) (2.1%, N = 90). Encounters with Coyotes (Canis latrans) (10.8%, N = 90) have been previously reported (Powers et al. 1984). Females of several closely grouped nests (seven nests within 100 m rad) were observed to defensively dive at Coyotes and Mule Deer (Odocoileus hemionus). Males, when present, would join in such defense but were never as vigorous (i.e., did not dive as low or as prolonged) as females after eggs hatched. Deer were suspected of trampling one nest in the study area.

Habitat Use—Males. Due to problems in visual and radio-tracking, home ranges for male harriers could only be approximated. Enderson and Kirven (1983) discuss problems in radio-tracking Peregrine Falcons (*Falco peregrinus*), similar to those encountered during this study. The estimated minimum mean home range for males of the four study nests was 15.7 km² (range 9.7–17.7 km²).

Chi-square (χ^2) analyses were made for each habitat type occurring at various distances from the nests in order to compare expected habitat use by males to available habitat in the study area (after Nicholls and Warner 1972). Male harriers used riparian habitats significantly more (P = 0.01) and shrubsteppe habitat significantly less (P = 0.01) than expected. The dominant habitat type in the study area was shrub-steppe (67.5%) with riparian habitat relatively uncommon (5.9%), but males frequented riparian habitat most often (43.9%) (Table 4). If irrigated cultivated fields are considered similar to riparian habitats based on availability of free water (Thomas et al. 1979), male activities in riparian-like habitats increases to 66.2% of total observations. Male activity in shrub-steppe habitat were limited to 17.7% of total observations (Table 4).

A total of 20 observations of males with identifiable prey items were recorded. An apparent shift from mammalian prey to reptilian prey appeared to be associated with alfalfa growth. All voles delivered by males to the nest or female (30% of total prey items) were observed prior to alfalfa growth of 46 cm. Following alfalfa growth to 46 cm in height, males delivered mostly Western Whiptails (*Cnemidophorus tigris*) (35% of total prey items). Other prey items identified included the Kangaroo Rat (*Dipodomys* sp., 15%), Deer Mouse (*Peromyscus maniculatus*, 5%), juvenile Nuttall's Cottontail (*Sylvilagus nuttallii*, 10%), Red-winged Blackbird (*Agelaius phoeniceus*, 5%) and showed no patterns associated with changes in vegetation height.

Male harrier activities in alfalfa fields were negatively correlated with vegetation height (r = -0.857, P < 0.05). However, activities in shrub-steppe habtat were positively correlated with alfalfa height (r = 0.914, P < 0.05). These relationships suggest a shift in habitat preference by hunting male harriers to more open shrub-steppe habitats as alfalfa growth approached an average height of 46 cm. Further, a distinct increase can be observed in harrier activities in shrub-steppe habitat after hatching of young (Table 4). Male harriers from three of the four study nests were observed in this apparent habitat and prey shift. The first cutting of alfalfa fields occurred about 1 June when alfalfa growth reached an average height of 61 cm. Following cutting of alfalfa, males appeared to return to the fields to hunt, but this could not be quantified before the study terminated. No other significant patterns were observed between harrier activities and habitat types.

Habitat Use—Females. Minimum home range size for the two study females was estimated at 1.13 km². Females were observed only in riparian and cultivated habitats directly adjacent to nests.

Females were observed with only two prey items:

a vole, and a Red-winged Blackbird caught in midair from a mobbing flock as it passed below the female's plane of flight. A similar response by female harriers to mobbing has been reported by England (1986).

DISCUSSION

Habitat Use and Foraging Behavior. Habitat use by harriers has been discussed by Nieboer (1973), Schipper (1973, 1977) and Watson (1977), mostly in reference to sympatric occurrence with other harrier species. Northern Harriers in North America are typically associated with lowlands, brackish or fresh water marshes, and mesic grasslands (Bent 1937; Brown and Amadon 1968; Apfelbaum and Seelbach 1983). Additionally, harriers are found in upland habitats distant from water sources (Rees 1976; Duebbert and Lokemoen 1977; Call 1978; Thurow et al. 1980; Thompson-Hanson 1984; Ryser 1985). In the Palearctic the Hen Harrier usually occupies drier open grasslands (Cramp 1908; Harrison 1982). Watson (1977) suggests that harriers secondarily occupy lowlands in North America due to a lack of competition with other harrier species.

Although the few prey items observed in this study are peripheral to the initial objective of determining habitat utilization, they collaborate with previous studies showing breeding harriers to be highly dependent on certain prey species, principally voles (Craighead and Craighead 1956; Hamerstrom 1969, 1979, 1986; Barnard 1983; MacWhirter 1985), and indirectly indicate foraging patterns and habitat use.

When temporal changes occur in prey densities, predators have been observed shifting to the second highest prey density (Taylor 1984). MacWhirter (1985) found nesting harriers at Tantramar Marsh, New Brunswick, principally predating voles but observed a significant shift to fledging passerines in late-June and early-July. Barnard (1983) also observed a significant prey shift, from voles to passerines. Errington (1933) and Errington and Breckenridge (1936) observed prey shifts, resulting in a succession of prey species appearing in the diet of harriers through the breeding season. However, Watson (1977) implies that any abundant population readily accessible to harriers may be substituted as prey. If voles are rare or absent, harriers prey on birds, primarily passerines (Schipper 1973, 1977; Watson 1977; Picozzi 1978; Barnard 1983; MacWhirter 1985). Rees (1976) observed nesting harriers in shrub-steppe habitats of eastern Washington preying exclusively on vole populations.

Data collected by Diller and Johnson (1982) indicate that riparian habitats support the greatest number of vertebrate species. Montan (1977) observed the greatest rodent numbers in the BOPA in riparian zones, with microtine species found only in wet sites such as riparian or irrigated cultivated habitats. It may be assumed that voles are limited in the BOPA due to the predominantly xeric environment. I found evidence of voles (i.e., runways, cuttings, and actual observations) only in riparian habitats including adjacent greasewood understory. Diller and Johnson (1982) observed only moderate numbers of Western Whiptails in greasewood and riparian habitats, and low numbers in big sagebrush habitats. However, they predicted that whiptails had the greatest potential as a prey species due to their ubiquity and relatively high mean biomass (g/ha). I observed Western Whiptails only in shrub-steppe habitats, but no effort was made to determine numbers in this or other habitat types.

Craighead and Craighead (1956) found raptor numbers directly related to prey vulnerability but not related to prey density. Wakeley (1979), Bechard (1982) and Janes (1985) suggest that factors other than prey availability or density, such as vegetative cover or structure, may influence foraging patterns by raptors. Errington and Breckenridge (1936) noted that alteration of vegetation structure, such as mowing, increased vulnerability of some prey species to predation by harriers. Montan (1977) noted that irrigated wheat fields attracted breeding deer mice and voles, but wheat is harvested only once and grows to a height which renders prey less vulnerable to predation. In contrast alfalfa is harvested several times during its growing season, continually altering vegetation structure and density. As indicated in this study, voles were predated in alfalfa fields prior to vegetation height of 46 cm and after cutting of alfalfa fields. The shift to Western Whiptails is probably a response to the reduced vulnerability of voles. Diller and Johnson (1982) observed that habitats with high lizard densities had relatively low percent ground cover with many areas of open ground or rocks. Such habitat characteristics would probably increase vulnerability of Western Whiptails to predation by harriers

Rice (1982) demonstrated that harriers depend heavily on auditory cues to locate prey. Harriers may be at a disadvantage in locating or capturing prey in high, dense vegetation similar to alfalfa >46 cm. Difficulty in plunging through dense vegetation to capture prey may also be a major disadvantage, allowing escape time for potential prey. Both vole and lizard movements were highly audible in natural habitats to 2.0 m (pers. observ.).

Harriers appeared to prey upon high density, vulnerable vole populations in riparian-like habitats. When vole vulnerability to predation decreased, harriers shifted to low density, relatively high biomass Western Whiptail populations vulnerable to predation in open shrub-steppe habitats.

Temeles (1986) observed partitioning of foraging behaviors and habitat utilization between sexes in wintering harriers. Observations of males and females foraging in different directions from nests suggests that foraging behavior and habitat differences between sexes may continue during the breeding season, except when females are dependent on mates provisioning prey.

Home Range. Previous studies have observed male harriers hunting 4.0-7.0 km from the nest and may range even farther (Schipper 1973, 1977; Watson 1977; Barnard 1983; Thompson-Hanson 1984). Home range sizes observed in the BOPA differ considerably from those observed by Breckenridge (1935), who estimated 2.49 km² to be an individual home range for harriers in mesic habitats of Minnesota. Craighead and Craighead (1956) estimated home range for breeding harriers at 2.1 km² (range 0.6–6.3 km²). Hamerstrom and De La Ronde Wilde (1973) and Picozzi (1978) estimated a home range for a breeding pair to be 8.8 km² and 14.0 km², respectively. Schipper (1977) observed home ranges of males sympatric with other harrier species varying from 1.8–12.3 km² (\bar{X} = 4.97 km²). Balfour (1962) estimated harrier hunting ranges in Orkney with no sympatric competitors to be 66.4 km². Thompson-Hanson (1984) found male home ranges in the shrubsteppe of eastern Washington varied from 72.1-366.0 km².

Minimum home ranges estimated for females in this study are similar to those observed by Craighead and Craighead (1956) and Schipper (1977). Watson (1977) noted that females usually hunt a smaller area than males, but Balfour (1957) observed a female at eight km from a nest with young.

Thompson-Hanson (1984) critically reviewed field methods and various analyses of radiotelemetric data JOHN W. MARTIN

for determining home range size for harriers, concluding that the minimum convex polygon method underestimates home range sizes. Swihart and Slade (1985) determined that nonstatistical methods, such as those used in estimating home ranges for harriers in this and other studies are valid, and that some statistical analyses may overestimate home range depending on the sampling interval of radio locations. However, large home ranges observed by Balfour (1962), Thompson-Hanson (1984) and this study may result from differences in habitat type and structure, or prey availability or vulnerability to capture. MacArthur and Pianka (1966), Schoener (1971, 1983) and Hixon (1980) predicted that the most probable response to a decrease in prey density is an increase in the foraging area.

Conclusion. Presuming the rationale of optimal foraging theory (Krebs et al. 1983), harriers may have visited relatively uncommon riparian and riparian-like (cultivated) habitats as long as foraging efforts were successful. When foraging efficiency declined, harriers shifted to common shrub-steppe habitat. After alteration of vegetation structure, increasing foraging efficiency of voles, harriers returned to riparian-like habitats. Rather than shifting specific search images of prey species (voles to lizards), harriers may have shifted foraging locations (riparian to shrub-steppe), each with differing prey species compositions. Such shifts in foraging location have been discussed by Royama (1970, 1971), Krebs et al. (1983) and Taylor (1984), or as a predator response to patchy or intermittent resources (Mac-Arthur and Pianka 1966). Male harriers selectively foraging in habitat types with an associated prey species easily captured may have been observed during this study. Additionally, with male harriers preferentially foraging a select percentage of available habitat types, large home ranges were observed.

ACKNOWLEDGMENTS

I am grateful for the field assistance of W. V. Sykora. I thank K. L. Bildstein, S. H. Broadbent, A. and J. Comer, F Hamerstrom, M. N. Kochert, C. D. Marti, B. and J. Martin, and K. Steenhof for their assistance, encouragement, and support. Also thanks to F. E. Andersen, P. E. Barnard, J. T. Flinders, M. N. Kochert, J. S. Marks, J R. Parrish, L. R. Powers, C. L. Pritchett, R. E. Simmons, K. Steenhof, and C. M. White for reviewing and commenting on drafts. Special thanks go to M. Martin who patiently followed this study through to its completion, and E. Abram and J. R. Parrish who typed or edited earlier drafts. Research was supported by the Snake River Birds of Prey Research Project, U.S. Bureau of Land Management, and the Zoology Department and Associated Students of Brigham Young University.

LITERATURE CITED

- ALTMANN, J. 1974. Observational study of behavior⁻ sampling methods. *Behaviour* 49:227-267.
- APFELBAUM, S. I. AND P. SEELBACH. 1983. Nest tree, habitat selection and productivity of seven North American raptor species based on the Cornell University nest record card program. *Raptor Res.* 17:97–113.
- BALFOUR, E. 1957. Observations on the breeding biology of the Hen Harrier in Orkney. *Bird Notes* 27:177–183, 216–224.
- ——. 1962. The nest and eggs of the Hen Harrier in Orkney. *Bird Notes* 30:69–73.
- BARNARD, P. E. 1983. Foraging behaviour and energetics of breeding Northern Harriers Circus cyaneus (L.). Unpubl. honrs. thesis, Acadia Univ., Nova Scotia, Canada.
- BECHARD, M. J. 1982. Effect of vegetative cover on foraging site selection by Swainson's Hawk. Condor 84:153-159.
- BENT, A. C. 1937. Life histories of North American birds of prey. Pt. 1. U.S. Nat. Mus. Bull. 167.
- BESKE, A. E. 1978. Harrier radio-tagging techniques and local and migratory movements of radio-tagged juvenile harriers. Unpubl. M.S. thesis, Univ. Wisconsin, Stevens Point.
- BILDSTEIN, K. L. 1979. Behavior of a pair of Northern Harriers on the day of nest abandonment. *Inland Bird Band. News* 51:63-65.
- ——. 1982. Responses of Northern Harriers to mobbing passerines. J. Field Ornith. 53:7–14.
- BRECKENRIDGE, W. J. 1935. An ecological study of some Minnesota Marsh Hawks. Condor 37:268-276.
- BROWN, L. AND D. AMADON. 1968. Eagles, hawks, and falcons of the world. McGraw-Hill Co., New York.
- BURKE, C. J. 1979. Effect of prey and land use on mating systems of harriers. Unpubl. M.S. thesis, Univ. W1sconsin, Stevens Point.
- CALL, M. W. 1978. Nesting habitats and surveying techniques for common western raptors. Bur. Land Manage. Tech. Note TN-316. Serv. Cent., Denver, CO.
- CRAIG, T. H., E. H. CRAIG AND J. S. MARKS. 1982 Aerial talon-grappling in Northern Harriers. *Condor* 84:239.
- CRAIGHEAD, J. J. AND F. C. CRAIGHEAD, JR. 1956 Hawks, owls, and wildlife. Stackpole Co., Harrisburg, PA.
- CRAIGHEAD, F. C., JR., J. CRAIGHEAD AND R. S. DAVIES 1963. Radio tracking grizzly bears. Pages 133-148. In L. E. Slater, ED. Biotelemetry: the use of telemetry in animal behavior and physiology in relation to ecological problems. Macmillan Co., New York.
- CRAMP, S. 1980. Handbook of the birds of Europe, the

Middle East, and North Africa. The birds of the western Palearctic. Vol. 2. Oxford Press, New York.

- DILLER, L. V. AND D. R. JOHNSON. 1982. Ecology of reptiles in the Snake River Birds of Prey Area. Contract Final Report, USDI, Bur. Land Manage., Boise, ID.
- DUEBBERT, H. F. AND J. T. LOKEMOEN. 1977. Upland nesting of American Bitterns, Marsh Hawks, and Shorteared Owls. *Prairie Nat.* 9:33-40.
- DUNSTAN, T. C. 1973. A tail feather package for radio tagging raptorial birds. Inland Bird Band. News 45: 3-6.
- ENDERSON, J. H. AND M. N. KIRVEN. 1983. Flights of nesting Peregrine Falcons recorded by telemetry. *Raptor Res.* 17:33-37.
- ENGLAND, M. E. 1986. Harrier kills mobbing Willet. Raptor Res. 20:78-79.
- ERICKSON, M. G. AND D. HOPPE. 1979. An octagonal bal-chatri trap for small raptors. *Raptor Res.* 13:36-38.
- ERRINGTON, P. L. 1933. Food habits of southern Wisconsin raptors: Part 2, hawks. Condor 35:19-29.
- AND W. J. BRECKENRIDGE. 1936. Food habits of Marsh Hawks in the glaciated prairie region of north-central United States. *Amer. Midl. Nat.* 17:831– 848.
- FYFE, R. W. AND R. R. OLENDORFF. 1976. Minimizing the dangers of nesting studies to raptors and other sensitive species. Canad. Wildl. Serv. Occas. Papers 23, Ottawa, Canada.
- HAMERSTROM, F. 1963. The use of the Great-horned Owl in catching Marsh Hawks. Proc. Internat. Ornithol. Congr. 13:866-869.
 - Band. News 40:43-46.
- ——. 1969. A harrier population study. Pages 367– 383. In J. J. Hickey, ED. Peregrine Falcon populations; their biology and decline. Univ. Wisconsin Press, Madison.
- ——. 1979. Effect of prey on predator: voles and harriers. Auk 96:370-374.
- -----. 1986. Harrier, hawk of the marsh: the hawk that is ruled by a mouse. Smithsonian Institute Press, Baltimore.
- AND D. DE LA RONDE WILDE. 1973. Cruising range and roost of adult harriers. Inland Bird Band. News 45:123-127.
- HAMMOND, M. C. AND C. J. HENRY. 1949. Success of Marsh Hawk nests in North Dakota. Auk 66:271-274.
- HARRISON, C. 1982. An atlas of the birds of the western Palearctic. Collins Ltd., London.
- HIXON, M. A. 1980. Food production and competitor density as the determinants of feeding territory size. *Amer. Nat.* 115:510-530.
- JANES, S. W. 1985. Habitat selection in raptorial birds.

Pages 159–188. In M. L. Cody, ED. Habitat selection in birds. Academic Press, New York.

- JENNRICH, R. I. AND F. B. TURNER. 1969. Measurement of non-circular home range. J. Theor. Biol. 22:227–237.
- KREBS, J. R., D. W. STEPHENS AND W. J. SUTHERLAND. 1983. Perspectives in optimal foraging theory. Pages 165–215. In G. A. Clark and A. H. Bruch, EDS. Perspectives in ornithology. Cambridge Univ. Press, Cambridge.
- LINNER, S. 1980. Resource partitioning in breeding populations of Marsh Hawks and Short-eared Owls. Unpubl. M.S. thesis, Utah State Univ., Logan.
- MACARTHUR, R. H. AND E. R. PIANKA. 1966. On optimal use of a patchy environment. *Amer. Nat.* 100: 603-609.
- MACWHIRTER, R. B. 1985. Breeding ecology, prey selection and provisioning of Northern Harriers *Circus cyaneus* (L.). Unpubl. honrs. thesis, Mt. Allison Univ. and Acadia Univ., Nova Scotia, Canada.
- MECH, L. D. 1983. Handbook of radio-tracking. Univ. Minnesota Press, Minneapolis.
- MOHR, C. O. 1947. Table of equivalent populations of North American small mammals. Amer. Midl. Nat. 37: 223-249.
- MONTAN, J. R., JR. 1977. Rodent density and species composition in the Snake River Birds of Prey Natural Area, Idaho. Unpubl. M.S. thesis, Utah State Univ, Logan.
- MUNOFF, J. A. 1963. Food habits, growth, and mortality in nesting Marsh Hawks. *Kingbird* 13:67-74.
- NICHOLLS, T. H. AND D. W. WARNER. 1972. Barred Owl habitat use as determined by radiotelemetry. J. Wildl. Manage. 36:213-224.
- NIEBOER, E. 1973. Geographical and ecological differentiation in the genus *Circus*. Ph.D. dissertation, Vrijie Univ. te Amsterdam.
- ODUM, E. O. 1971. Fundamentals of ecology. Saunders, Philadelphia.
- PICOZZI, N. 1978. Dispersion, breeding and prey of the Hen Harrier *Circus cyaneus* in Glen Dye, Kincardshirre. *Ibis* 120:498-509.
- POWERS, L. R., T. H. CRAIG AND J. W. MARTIN. 1984. Nest defense by Northern Harriers against the coyote in southwestern Idaho. *Raptor Res.* 18:78–79.
- REES, J. R. 1976. Behavioral ecology of Marsh Hawks in dissimilar habitats. Unpubl. M.S. thesis, Eastern Washington State Univ., Cheney.
- RICE, W. R. 1982. Acoustical location of prey by the Marsh Hawk: adaptation to concealed prey. Auk 99. 403-413.
- ROYAMA, T. 1970. Factors governing the hunting behaviour and selection of food by the Great Tit (Parus major L.). J. Anim. Behav. 39:610-668.
 - ------. 1971. Evolutionary significance of predators' response to local differences in prey density: a theoretical study. Pages 344-357. In P. J. Den Boer and

G. R. Gradwell, EDS. Proc. Adv. Study Inst. Dynamics Numbers Popul. Oosterbeek, Netherlands.

- RYSER, F. A., JR. 1985. Birds of the Great Basin. Univ. of Nevada Press, Reno.
- SCHARF, W. C. 1968. Improved technique for trapping harriers. Inland Bird Band. News 40:163-165.
- SCHIPPER, W. J. A. 1973. A comparison of prey selection in sympatric harriers (*Circus*) in Western Europe. Le Gerfaut 63:17-120.
- ——. 1977. Hunting in three European harriers (*Circus*) during the breeding season. *Ardea* 65:53–72.
- SCHOENER, T. W. 1971. Theory of feeding strategies. Ann. Rev. Ecol. Syst. 2:369-404.
- ------. 1983. Simple models of optimal feeding territory size: a reconciliation. *Amer. Nat.* 121:608-629.
- SNEDECOR, G. W. AND W. G. COCHRAN. 1967. Statistical methods. Iowa State Univ. Press, Ames.
- SWIHART, R. K. AND N. A. SLADE. 1985. Influence of sampling interval on estimates of home-range size. J. Wildl. Manage. 49:1019-1025.
- TAYLOR, R. J. 1984. Predation. Hall and Chapman, New York.
- TEMELES, E. J. 1986. Reversed sexual dimorphism: effect on resource defense and foraging behaviors of nonbreeding Northern Harriers. Auk 103:70-78.
- THOMAS, J. W., C. MASER AND J. E. RODIER. 1979.

Wildlife habitats in managed rangelands — the Great Basin of southeastern Oregon: riparian zones. For. Serv Gen. Tech. Rept. PNW-80. Pacific Northwest For and Range Exp. Stat., Portland, OR.

- THOMPSON, S. P. AND J. E. CORNELY. 1982. Nest provisioning behavior by a male Northern Harrier on the death of his mate. *Wilson Bull*. 94:564-566.
- THOMPSON-HANSON, P. A. 1984. Nesting ecology of Northern Harriers on the Hanford Site, south-central Washington. Unpubl. M.S. thesis, Washington State Univ., Pullman.
- THUROW, T. L., C. M. WHITE, R. P. HOWARD AND J. F. SULLIVAN. 1980. Raptor ecology of Raft River Valley, Idaho. U.S. Dept. Energy, Idaho Falls, ID.
- U.S.D.I. 1979. Snake River birds of prey special report. Bur. Land Manage., Boise Dist., Boise, ID.
- WAKELEY, J. S. 1979. Use of hunting methods by Ferruginous Hawks in relation to vegetation density. *Raptor Res.* 13:116-118.
- WATSON, D. 1977. The Hen Harrier. T. and A. D Poyser, Berkhamsted, England.
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Received 1 January 1986; Accepted 5 January 1987

22nd Annual Meeting of The Raptor Research Foundation, Inc.—The Raptor Research Foundation, Inc., will hold its annual meeting 28-30 October 1987 at the Red Lion Riverside Hotel, Boise, Idaho. The meeting will feature a symposium on migration of raptors in western North America. Karen Steenhof, Bureau of Land Management, 3948 Development Avenue, Boise, Idaho 83705, is the Program Committee Chairperson. Deadline for abstracts is 31 July. For more information contact the Conference Committee Chairman, Rich Howard, U.S. Fish and Wildlife Service, 4696 Overland Road, Room 576, Boise, ID 83705, telephone (208) 334-1888.